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A New *Acanthocyclops* KIEFER, 1927 (Copepoda: Cyclopoida) from Central Mexico with Comments on the Distribution of the Genus in Middle America

key words: limnology, Cyclopidae, diversity, crustacean zooplankton

Abstract

A new species of *Acanthocyclops* KIEFER is described from central Mexico. It differs from its congeners by a combination of characters including mainly: 11–13 antennular segments, a spine formula of 3444 and modified setae on legs 2–4. The presence of a compound distal antennular segment is aberrant within the Cyclopoida. The new species seems to be related to Nearctic forms of the *vernalis*–*robustus* clade. Ancestors of this lineage probably reached central Mexico as a result of glaciation events and the new species is a remain of stranded postglacial populations; some of these forms were successful in colonizing tropical lands. A key for the identification of the species of *Acanthocyclops* recorded in Mexico is included.

1. Introduction

The genus *Acanthocyclops* KIEFER, 1927 is among the five most speciose of the cyclopoid copepod subfamily Cyclopinae: there are more than 48 nominal species and subspecies of this genus known to date (DUSSART and DEFAYE, 1985; BOXSHALL and HALSEY, 2004). The knowledge of *Acanthocyclops* in the Americas is still scarce and biased. The number of species known in North America is the highest in the continent (12 species) (YEATMAN, 1959; REID *et al.*, 1991; REID, 1998; WILLIAMSON and REID, 2001), versus only 4 in South America (REID, 1985; ROCHA and BOTELHO, 1998). In Mexico, Central America, and the insular Caribbean, REID (1990a) recognized only two species of *Acanthocyclops*: *A. robustus* (SARS, 1863) and *A. vernalis* (FISCHER, 1853). More recently, two new species of this genus were described from material collected in southeastern Mexico (REID and SUÁREZ-MORALES, 1999; FIERS *et al.*, 2000).

It is widely recognized that some species groups show a high intraspecific morphological (DODSON, 1994; DODSON *et al.*, 2003) and genetic (GRISHANIN *et al.*, 2005) variability. This, together with incomplete descriptions, resulted in many species with an uncertain status (see REID *et al.*, 1991; EINSLE, 1996) and a progressively complex taxonomy that relies on only a few relatively stable characters. This tendency is shared by other genera in the subfamily Cyclopinae (ROCHA, 1998). One of the most relevant cases of taxonomical confusion includes *A. vernalis* and *A. robustus*, each of them probably representing a complex of cryptic species (DODSON *et al.*, 2003). Some of these are being described from different geographical areas (MIRABDULLAYEV and DEFAYE, 2002, 2004).

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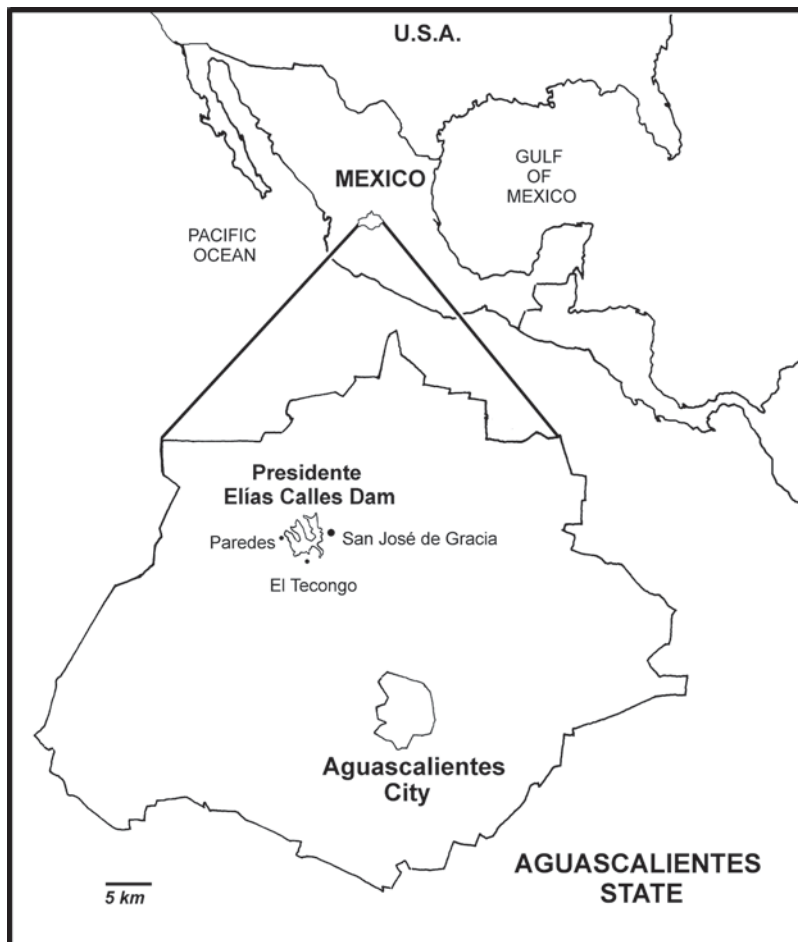


Figure 1. Location of the surveyed area in Aguascalientes, Mexico. The type locality of *Acanthocyclops dodsoni* n. sp. is the Presidente Elías Calles Dam.

Species of *Acanthocyclops* occur as littoral epibenthic forms in ponds, lakes and ground-water (REID *et al.*, 1991; FIERS *et al.*, 2000). In this contribution a new species of *Acanthocyclops* is described based on male and female specimens collected in a large dam in Aguascalientes, central Mexico. The significance of this finding is discussed in terms of the diversity and distributional patterns of the genus in the Nearctic and part of the Neotropical regions. A dichotomic key for the identification of the species known to be distributed in Mexico is also included.

The Presidente Elías Calles dam is located 30 km's northeast from the city of Aguascalientes, Central Mexico (Fig. 1). It is a large, permanent water body surrounded by crop vegetation and by a high mountain ridge 2000 m above the sea level. There are small urban areas adjacent to the dam.

2. Methods

During the development of a project to determine the diversity of cyclopoid copepods in the Mexican state of Aguascalientes, zooplankton samples were collected between 1989 and 2003 in more than 500 water bodies covering the whole state (see DODSON and SILVA-BRIANO, 1996). Samples were collected using a standard plankton net hauled near the shoreline of the ponds. The biological material was then fixed and preserved in 70% ethanol. Copepods were sorted out from the entire original biological samples and maintained in 70% ethanol with a drop of glycerine. Several male and female specimens of a species of *Acanthocyclops* were collected during this survey at one of the localities (Presidente Elías Calles Dam); based on a preliminar analysis, these copepods were tentatively identified as copepodites of *A. vernalis*. A second, closer examination of these specimens was performed in the laboratory during a recent course on copepod taxonomy, and differences with respect to *A. vernalis* motivated a deeper analysis. The structures with taxonomical relevance within the genus were evaluated based on REID (1985) and REID *et al.* (1991). Specimens were dissected and examined following the techniques described by WILLIAMSON and REID (2001) and REID (2003). Two females were dissected and two females and one male were prepared for SEM examination, including dehydration in progressively higher ethanol solutions (80, 96, 100%), drying, and coating following standard methods. All dissected specimens were mounted in semi-permanent slides with glycerine sealed with Entellan®, a commercial, fast drying mounting medium and sealant. Scaled drawings were done at 40X magnifications with a drawing tube mounted on a standard Olympus CX31 microscope.

This hitherto unknown species was described and illustrated following the current standards for the taxonomic study of the genus (EINSLE, 1996; FIERS *et al.*, 2000). Emphasis was given to describe the ornamentation of the coxal plates and the armature of the swimming legs and the caudal rami, including the length and proportions of the caudal setae and the structure of the fifth legs. The specimens of the new species were deposited in the collection of zooplankton held in El Colegio de la Frontera Sur (ECO-CH-Z), in Chetumal, Mexico and in the Laboratory of Ecology of the University of Aguascalientes, Mexico.

3. Results

Order: Cyclopoida G. O. SARS, 1886

Family: Cyclopidae BURMEISTER, 1834

Subfamily: Cyclopinæ BURMEISTER, 1834

Genus: *Acanthocyclops* KIEFER, 1927

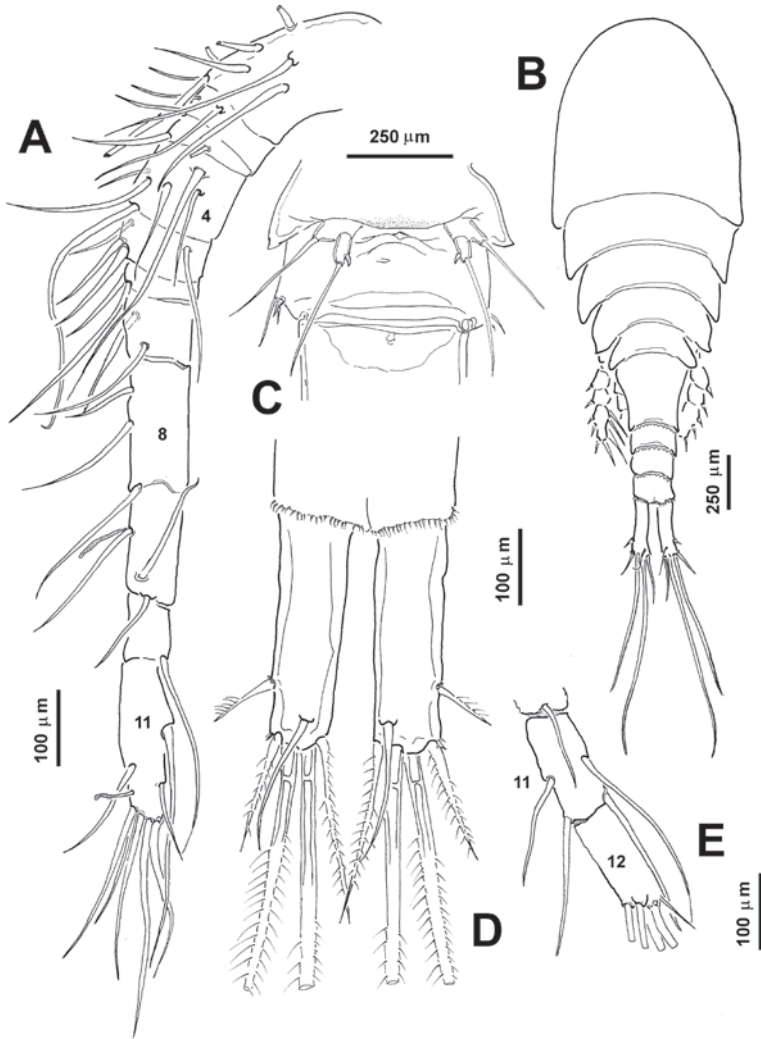
Acanthocyclops dodsoni MERCADO and SUÁREZ-MORALES, n. sp.

(Figs. 2–6)

Material examined. – Holotype. Adult ♀, dissected, mounted in glycerine sealed with Entellan (ECOCH-Z-02956), Presidente Elías Calles Dam, Aguascalientes, Central Mexico. January 19, 1989; coll. Marcelo Silva-Briano. Allotype. 1 adult ♂, undissected, same locality, collector, and date, ethanol-preserved, vial (ECOCH-Z-02957). Paratypes. 4 adult ♀♀, 1 undissected adult ♂, ethanol-preserved, in vials, same locality and date (ECOCH-Z-02959, ECOCH-Z-02958). 5 undissected adult ♀♀, ethanol-preserved, in vial, same locality and date, coll. Marcelo Silva-Briano. Latter specimens deposited, together with original samples, specimens treated for SEM observation, and additional material from type locality, in collection of M. Silva-Briano at University of Aguascalientes.

Type locality. – Presidente Elías Calles Dam (22°10'45" N; 102°28'00" W), Aguascalientes, central Mexico.

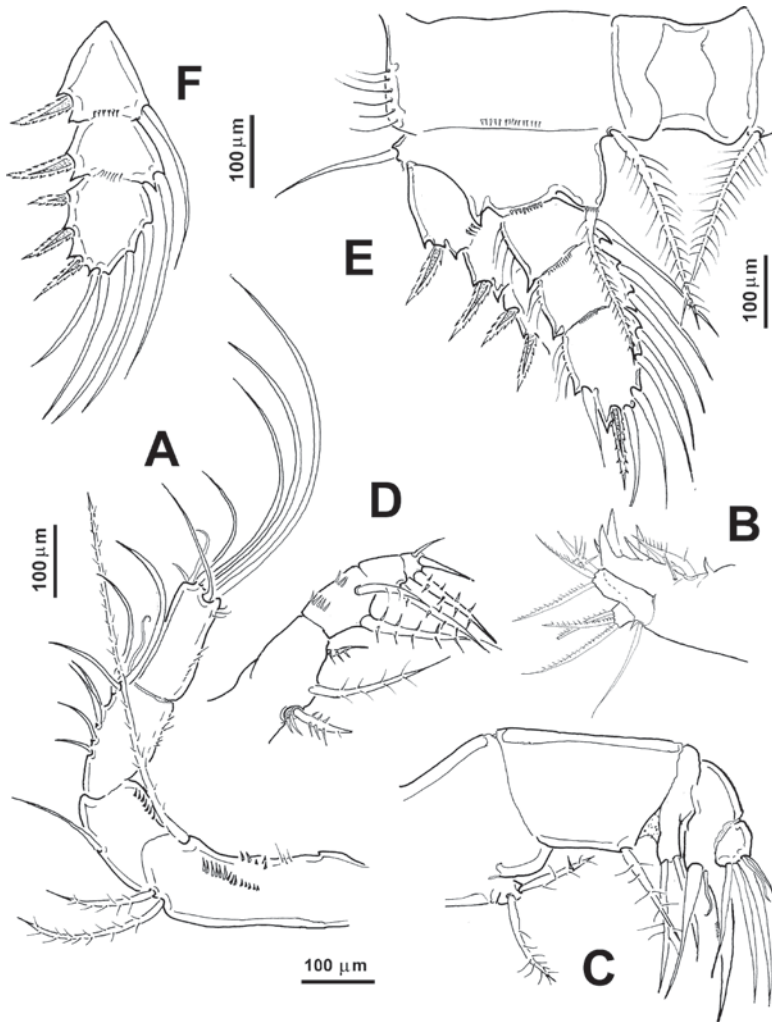
Etymology.– The species is warmly dedicated to Dr. STANLEY I. DODSON for his many contributions to understand the biology and taxonomy of the genus *Acanthocyclops*.



Figures 2A–D. *Acanthocyclops dodsoni* n. sp. adult female. A) antennule; B) habitus, dorsal view; C) fifth pedigerous and genital double-somites, ventral view; D) caudal rami, dorsal view; E) distal segments of 12-segmented antennule.

3.1. Descriptions

Female (Fig. 2B): Total body length = 2.11 ± 0.125 mm ($n = 7$) from anterior end of cephalothorax to posterior margin of caudal rami. Body robust, cephalothorax relatively long, slightly expanded laterally at midlength of cephalosome in dorsal view; lateral margins of pedigers 3 and 4 straight, produced posteriorly. Cephalothorax length = 0.130 ± 0.07 mm ($n = 7$), representing 62% of total body length. Dorsal surface smooth, antennules reaching end of first pediger. Urosome relatively slender, formed by 5 somites: fifth pediger plus 4 succeeding somites. Genital double-somite moderately

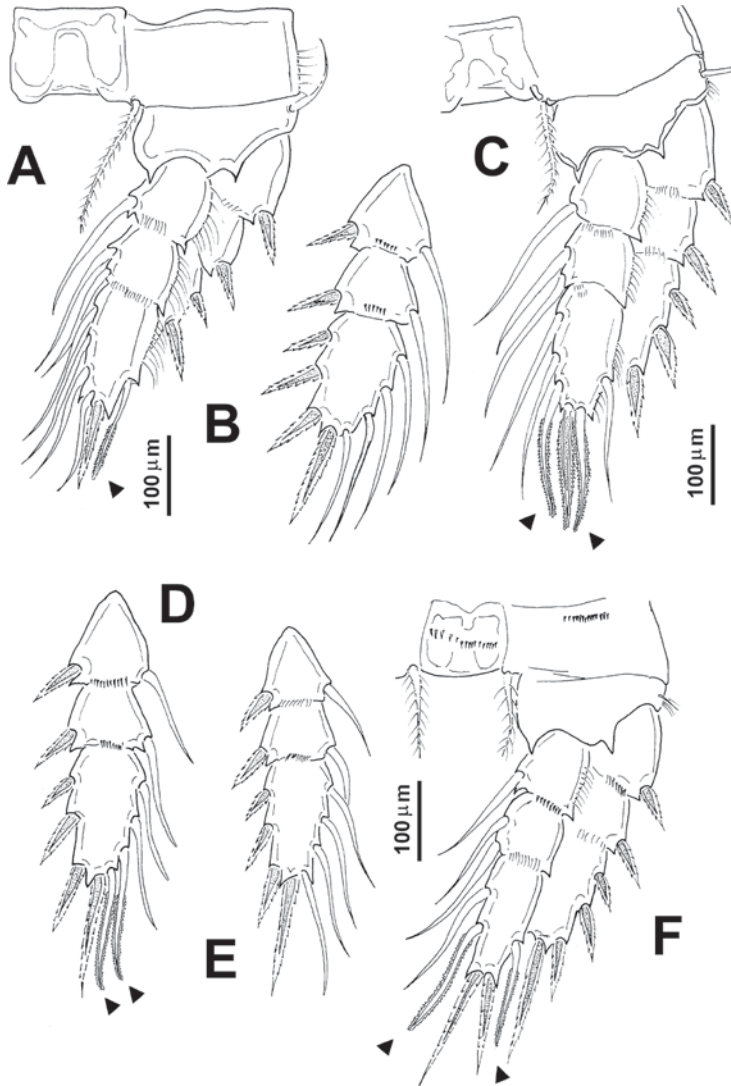


Figures 3A–E. *Acanthocyclops dodsoni* n. sp. adult female. A) antenna; B) maxillule; C) maxilla; D) maxilliped; E) leg I and coupler; F) exopod of leg 1.

expanded at proximal half. Anal and preanal somites equally sized. Urosome, including caudal rami, representing 38% of body length.

Antennule (Fig. 2A): 11–12 segmented in most specimens; armament per segment as follows (s = seta, ae = aesthetasc): 11-segmented: 1(8s), 2(3s), 3(2s), 4(6s), 5(4s), 6(2s), 7(2s), 8(3s), 9(3s + ae), 10(1s), 11(8s + ae); 12-segmented: 1(8s), 2(2s), 3(8s), 4(1s), 5(1s), 6(1s), 7(2s), 8(1s), 9(1s), 10(1), 11(4s), 12(5s). Some specimens with 13 antennular segments: 1(7s), 2(3s), 3(2s), 4(2s), 5(2s), 6(2s), 7(3s), 8(2s), 9(2s), 10(1s + ae), 11(3s), 12(4s), 13(10s). Antennule reaching middle of second thoracic somite.

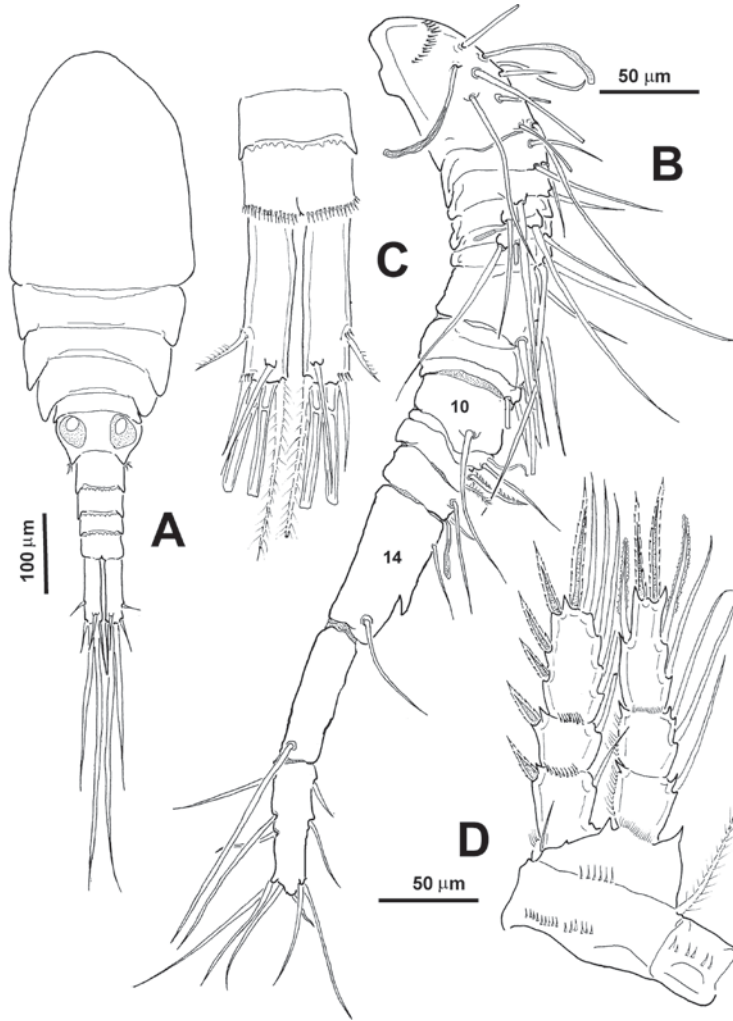
Antenna (Fig. 3A): Four-segmented, basis with two groups of unsocketed spines on caudal surface. Largest spines arranged longitudinally on medial position, additional group adja-



Figures 4A–F. *Acanthocyclops dodsoni* n. sp. adult female. A) leg 2 and coupler; B) exopod of leg 2; C) leg 3 and coupler; D) exopod of leg 3; E) exopod of leg 4; F) leg 4 and coupler. Arrows indicate modified setae on swimming legs.

cent to first one, with a few spines of same size. Basis with long exopodal seta biserially pinnate plus two basipodal setae equal in size. First segment of endopodite with single outer seta and inner row of 5–7 spinules. Second segment of endopodite with 4 lateral and 4 terminal outer setae; inner margin with row of short hair-like setules. Third endopodal segment with 7 terminal setae, with subterminal tuft of setules.

Labrum (Fig. 6A): Distal margin with 9 blunt teeth between rounded lateral protuberances; 2 rows of long, slender spines on ventral surface.

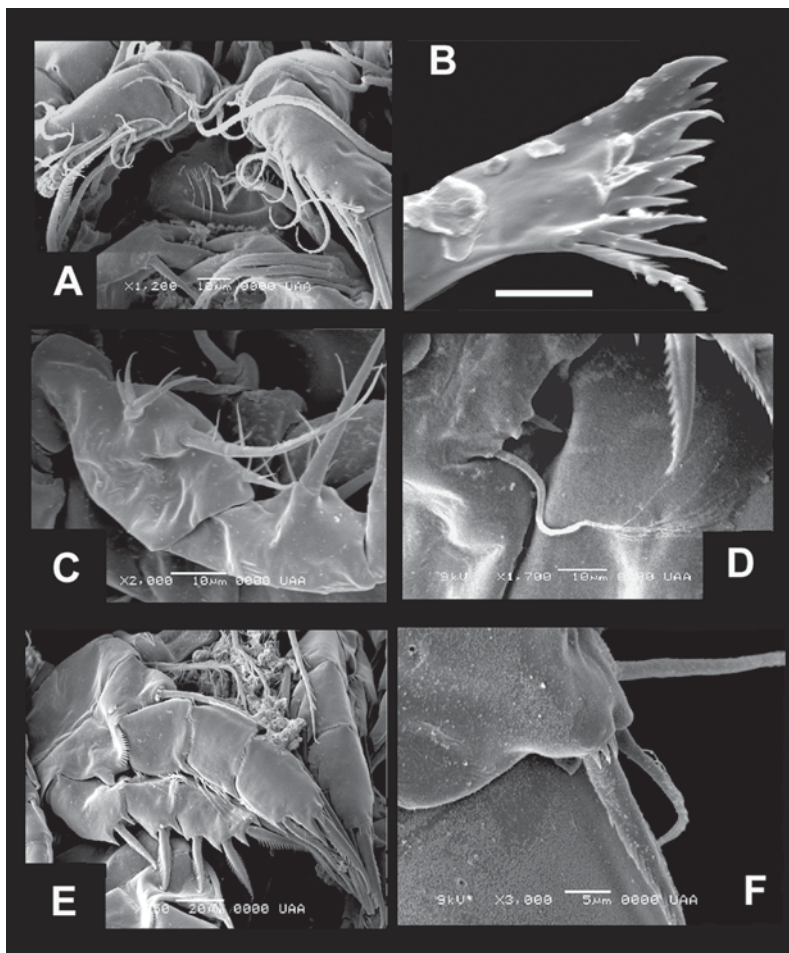


Figures 5A–D. *Acanthocyclops dodsoni* n. sp. adult male. A) habitus, dorsal view; B) antennule; C) caudal rami, dorsal view; D) leg 4 and coupler.

Mandible (Fig. 6B): Gnathobase with 9 strongly chitinized teeth and long dorsal seta armed with inner row of spinules. Palp reduced, with 2 long biserially plumose setae and 1 hair-like seta about half the length of two setae.

Maxillule (Fig. 3B): Precoxal arthrite with surface naked, with 3 strong chitinized claws and 2 spiniform setae on frontal side. Basis of palp furnished apically with one long spine bearing row of spinules and two stout setae. Endopod subquadrate, with three unequally long apical setae; spiniform process present near base of long exopodal seta.

Maxilla (Fig. 3C): Precoxa and coxa not fused; precoxal endite armed with 2 strong biserially setulated setae. Coxa with single long seta on distal inner margin; coxal caudal surface naked. Proximal basipodal endite well developed, with 2 apical seta furnished with spinules, one noticeably thicker than the other. Claw-like basal endite relatively short, bearing



Figures 6A–F. *Acanthocyclops dodsoni* n. sp. A–D: adult female, E–F: adult male, SEM. A) inner surface of first antennal segment and labrum, ventral view; B) mandible, gnathobase; C) first and second segments of maxilliped; D) sixth legs; E) leg 1 showing ornamentation; adult male F) sixth leg plate and basal ornamentation. Bar in Figure B represents 10 μ m.

short inner row of 6 spinules; endite with two setae, one large, one small, slender both inserted near base of claw. Endopod 1-segmented, with 3 strong, long spiniform setae plus 2 short, slender setae.

Maxilliped (Figs. 3D, 6C): Four-segmented. Syncoxa with three spiniform setae along inner margin: the proximal one has four spinules at its insertion, middle one longest. proximal group of 3 short, strong setae bearing spiniform setules, distalmost seta longest, twice as long as accompanying setae. Basis with two spiniform setae, and two transversal rows of spines. Endopod reduced, 2-segmented, first segment with wide-based, stout basal spine sparsely spinulated. Second endopod armed with 3 elements: 1 proximal strong, spiniform seta, 1 strong seta, unarmed; third seta short, relatively slender, about 1/4 the length of proximal seta.

Table 1. Armature of swimming legs 1–4 (spines in Roman numerals, setae in Arabic) of *Acanthocyclops dodsoni* n.sp. Sequence follows inner to outer positions.

	coxa	basis	exopodite	endopodite
leg 1	1–0	1–1	I-1; I-1; III,2,2	1–0; 2–0; 3,1-I,1
leg 2	1–0	0–1	1-I; 1-I; 2,2,III	1–0; 2–0; 3,1-I,1
leg 3	1–0	0–1	1-I; 1-I; 3,1-I,III	1–0; 2–0; 3,2,1
leg 4	1–0	0–1	1-I; 1-I; 3,1-I,III	1–0; 2–0; 2,II,1

Leg 1 (Figs. 3E, F, 6E): Intercoxal sclerite (coupler) naked, distal margin with 2 rounded chitinized projections. Coxa with strong, biserially setulated inner coxal seta, row of 5–6 long hair-like setae on outer margin, and row of spinules along distal margin. Basis with 1 slender basipodal seta on outer margin, inner margin moderately expanded, with strong, spiniform basipodal seta reaching midlength of third endopodal segment; small spines at insertion of inner basipodal seta and along insertion of endopod. Endopod and exopod 3-segmented. Endopod slightly longer than exopod. Armature as in Table 1.

Leg 2 (Figs. 4A,B): Intercoxal sclerite (coupler) with distal margin naked, with 2 rounded chitinized projections. Coxal surface naked, with strong, inner coxal spiniform seta plus row of hair-like setules along outer margin. Basis with 1 slender seta on outer margin; inner corner and middle margin of basis forming spiniform expansions. Endopod and exopod 3-segmented. Endopod nearly as long as exopod. Subdistal outer seta of third endopodal segment modified, stout, with short, spiniform setules (arrowed in Fig. 4A). Armature as in Table 1.

Leg 3 (Figs. 4C, D): Intercoxal sclerite (coupler) as in leg 2. Coxa with inner coxal seta. Basis with biserially setulated seta on outer margin, row of short hair-like setae near insertion of seta; inner corner and middle margin of basis forming spiniform expansions. Endopod and exopod 3-segmented. Endopod slightly longer than exopod. Two modified setae on each terminal endopodal (arrowed in Fig. 4C) and exopodal (arrowed in Fig. 4D) segments. Armature as in Table 1.

Leg 4 (Figs. 4E, F): Intercoxal sclerite (coupler) showing single row of 15–20 spinules on anterior surface; distal margin smooth, not expanded. Coxal surface with proximal and distal transverse rows of small spiniform elements; inner coxal seta relatively shorter than that of legs 1–3. Basis with 1 slender seta on outer margin, with hair-like tuft of setae near insertion point. Endopod and exopod 3-segmented. Endopod slightly longer than exopod. Armature as in Table 1. Outer and inner terminal endopodal spines dentate along most of margins. Inner and outer spines subequal in length and width; length ratio of outer and inner terminal spines of Enp 3 = 0.93. Length/width ratio Enp 3 = 2.6. Insertion point of seta on outer margin of Enp 3 = 0.57 of the length of segment. Length of inner endopodal spine/endopod 3 = 0.94. Third exopodal segment with 4 outer spines. Subdistal inner and outer endopodal setae modified (see Fig. 4F).

Leg 5 (Fig. 2C): Leg consisting of two free segments, first (proximal) subrectangular, with moderate lateral expansion bearing long regular seta; second (distal) segment about 1.6 times longer than broad, bearing long sparsely setulated seta inserted distally. Short spiniform element inserted subdistally; spiniform element barely reaching distal margin of segment.

Leg 6 (Fig. 6D): Small, low plate near lateral margin of genital double-somite with relatively long lateral seta, and 2 short spines, middle spine slightly longer than medial spine.

Urosome (Figs. 2B, C): Posterior margins of genital double somite, urosomites, and anal somite crenulated both dorsally and ventrally; relative ratio of each urosomite as: 45.7: 17: 18.6: 18.6 = 100. Genital double-somite representing 14% of body length (excluding caudal rami). Genital double-somite smooth on ventral and dorsal surfaces. Anterior half of genital

double-somite expanded laterally. Seminal receptacle with 2 short lateral arms; lateral channels straight. Ventral surface of anal somite smooth; distal ventral and dorsal margins with rows of 15–18 stout spines at insertion points of caudal rami.

Caudal ramus (Fig. 2D): Ramus representing 12.5% of total body length and 0.45 times as long as urosome. Length/width ratio = 4.2. Inner and outer margins smooth, unornamented. Cluster of minute spines at base of lateral spiniform seta and near base of outer terminal seta. Lateral terminal spiniform seta short, 0.17 times as long as caudal ramus, inserted at about 2/3 of the outer margin of ramus. Dorsal seta relatively short, 0.6 times as long as caudal ramus. Inner terminal seta 0.8 times as long as caudal ramus; seta slightly longer than dorsal seta. Inner terminal seta longest, about 30% longer than outer terminal seta.

Male (Figs. 5A–D): Mean length of Aguascalientes specimens: 0.62 mm, length of allotype 0.672 mm. Caudal rami, antenna, mouth parts, legs 1–5 as in female. Habitus similar to females, except urosome segmentation and relative size. Antennule geniculate, of 16 segments; distal ancestral segments segments XXIV–XXVIII (see HUYS and BOXSHALL, 1991) fused. Spiniform expansion on segment 14 only. General setation pattern as in *A. montana* (REID *et al.*, 1991), except for one aesthetasc less on first and ninth segments. Leg 4 ornamentation of coxal plate weaker than in female, coxal seta slightly longer. Leg 6 consisting of small, subrectangular indistinctly separated plate armed with 4–5 spinules at base of stout inner spine, middle seta short, outer seta about twice as long as stout spine (Fig. 6F).

Remarks: The antennule of this species shows an important range of variation both in terms of segmentation and setation patterns. Out of the specimens available to us about half have 11 antennular segments, 40% bear 12, and 10% have 13-segmented antennules. According to the known patterns of antennular morphology, the 11-segment pattern in cyclopine copepods results from the fusion of segments 3–4, 8–11, and 12–14 of the basic 17-segmented state. The latter two fusions of segments are expressed in our specimens with 11 antennular segments (3 setae on segment 8 representing fusion of 8–11; 3 setae plus aesthetasc on segment 9, by fusion of segments 12–14). Apparently, there is no fusion of distal segments 16–17 in the 11-segmented pattern. The first fusion (segments 3–4) is expressed in specimens with 12 antennular segments (8 setae on third segment), but not in the 13-segmented specimens; the other segments appear to have reductions in the number of setal elements thus making it difficult to follow the fusion patterns, but some of distal four segments are probably fused in these specimens. Most importantly, however, basic segments 16–17 are fused in two of the patterns (11 and 13 segments) as shown by the presence of a large compound distal segment with two setae on the internal surface and no traces of arthrodistal membrane on it. This pattern is aberrant in the Cyclopinae (see HUYS and BOXSHALL, 1990; SCHUTZE *et al.*, 2000) and differs from all other species of the genus where these two distal segments are always separated. Only in the 12-segmented specimens the arthrodistal membrane expressing the segmental division is clearly present.

4. Discussion

The general body shape, the armature of the swimming legs, and the setation of the fifth leg of the new species are similar to other members of the genus *Acanthocyclops*. As stated by EINSLE (1996), some of these characters show strong affinities with related cyclopine genera such as *Megacyclops* KIEFER, 1927 and *Cyclops* O. F. MÜLLER, 1785. The main characters of the new species, which allow to include it in the genus *Acanthocyclops* are: 1) fifth leg represented by two segments, the distal one armed with a small subapical spine reaching the distal end of basal segment; 2) antennule with less than 17 segments; 3) inner margin of caudal rami naked (see REID, 1985; EINSLE, 1996; DUSSART and DEFAYE, 2001).

Following the criteria proposed by REID *et al.* (1991) and EINSLE (1996) the species of *Acanthocyclops* are first characterized by the number of antennular segments in the females;

most species are 17-segmented, a smaller group is 12-segmented, another reduced group of species share an 11-segmented antennule, and only one has 14 segments (see EINSLE, 1996). Most of the female specimens of *A. dodsoni* n. sp. have 11 antennular segments, although some specimens have 12 or even 13 segments; hence, it is compared herein with all other species having these patterns. There are several other nominal species apparently always having 11 antennular segments: *A. kieferi* (CHAPPUIS, 1925), *A. reductus* (CHAPPUIS, 1925), *A. exilis* (COKER, 1934), *A. hispanicus* KIEFER, 1937, *A. notabilis* MAZEPOVA, 1950, *A. profundus* MAZEPOVA, 1950, *A. biarticulatus* MONCHENKO, 1972, *A. sambugarae* KIEFER, 1981, *A. petkovskii* PESCE and LATTINGER, 1983, *A. similis* FLÖSSNER, 1984, *A. parvulus* STRAYER, 1988, *A. balcanicus* NAIDENOV and PANDOURSKI, 1992, and *A. raidevi* PANDOURSKI, 1993 (see REID *et al.*, 1991; EINSLE, 1996; REID and SUÁREZ-MORALES, 1999). A useful character to separate *A. dodsoni* n. sp. from these other 11-segmented forms is the length and proportions of the inner terminal caudal seta (EINSLE, 1996). In the new species this seta is shorter than the caudal ramus, the same pattern shown by *A. kieferi*, *A. reductus*, and *A. parvulus*. Differences with respect to these species are: 1) the length of the dorsal caudal seta, shorter than the inner seta; 2) the relative length of the terminal spines of the third endopod of leg 4, almost equal in the new species and with markedly different sizes in *A. kieferi* and *A. reductus*; 3) the spine formula of the third exopod of swimming legs 1–4, 2333 in all these species, 3444 in the new species. Of the remaining species with 11 segments, *A. petkovskii* and *A. sambugarae* have a distinctive inner terminal caudal seta, noticeably longer than the ramus; this seta is clearly shorter than the caudal ramus in the new species. Also, the caudal ramus of these two species is shorter and more robust than it is in *A. dodsoni* (EINSLE, 1996, Figs. 37, 38). The new species differs from *A. hispanicus* and *A. exilis* in the proportional lengths of the inner and outer terminal caudal setae (see EINSLE, 1996) and by having a set of terminal spines of the fourth leg endopod subequal in size, whereas these spines are clearly unequal in the latter two species. *Acanthocyclops raidevi* and *A. balcanicus* have 2-segmented endopodites on legs 1 and 2, thus differing from the 3-segmented condition of the new species. The spine formula and the presence of several modified setae on legs 2–4 are probably the most important characters to distinguish the new species; in fact, *A. dodsoni* is the only species of *Acanthocyclops* known to combine 11-segmented antennules with a 3444 spine formula.

Some specimens of *A. dodsoni* n. sp. have 12-segmented antennules. The new species differs from the group of species of *Acanthocyclops* with 12-segmented antennules: *A. gmeineri* POSPISIL, 1989, *A. montana* REID and REED, 1991, *A. pennaki* REID, 1992, *A. rhenanus* KIEFER, 1936, *A. muscicola* (LASTOCHKIN, 1924), *A. venustoides* COKER, 1934, *A. venustus* NORMAN and SCOTT, 1906, *A. capillatus* (SARS, 1863) (see EINSLE, 1996) by having 4 inner setae on the third exopodal segment of legs 1–4, a 3444 spine formula, an inner terminal caudal seta shorter than caudal ramus, a dorsal seta shorter than the inner terminal seta, inner margin of caudal rami naked (see EINSLE, 1996). The 12-segmented specimens from Aguascalientes key down to *A. venustoides* in EINSLE's (1996) key; the new species diverges in having a naked inner margin of caudal ramus, a set of modified setae on the swimming legs, and a 3444 spine formula. There is only one other known species of the genus with 13-segmented antennules, the Russian *A. muscicola* (LASTOCHKIN, 1924), which has 12–13 antennular segments (EINSLE, 1996); the Nearctic *A. columbiensis* REID, 1990 (REID, 1990b) has 14 antennular segments.

There are only two North American species of *Acanthocyclops* with 11-segmented antennules: *A. exilis* and *A. parvulus* (REID *et al.*, 1991; WILLIAMSON and REID, 2001). These species also share with *A. dodsoni* n. sp. a naked inner margin of the caudal rami, and particularly with *A. parvulus*, subequal terminal spines of the third endopod of leg 4. The new species seems to have affinities also with the North American *A. montana* (with 12-segmented antennules), including the spine (3444) and setal formulas (4444), naked inner margin of caudal ramus, and subequal lengths of terminal spines of third endopodal segment of

leg 4 (see REID *et al.*, 1991). Aside the antennular segmentation, the new species differs from *A. montana* in 1) the shape and size of the genital somite: clearly robust and expanded laterally in *A. montana*, relatively slender in the new species; 2) a relatively shorter inner terminal caudal seta, 1.2 times as long as caudal ramus *vs* 0.8 in *A. dodsoni* n. sp.; 3) the ornamentation of the antennal basipod is different in both species, with two well-defined longitudinal rows of strong spinules in the new species *vs* a single transverse row and two clusters of small spinules in *A. montana* (see REID *et al.*, 1991, Figs. 31, 32); 4) the new species has spines at the insertion of lateral caudal seta and outer terminal seta, whereas these ornamentations are absent in *A. montana*; 5) the coxal plate of legs 4 of *A. montana* is naked *vs* a medial row of spinules in the new species. 6) the inner corner of the basipodite of leg 4 is produced into a spiniform process in the new species, it is relatively unmodified in *A. montana*. The new species is also similar to *A. michaelseni* (MRÁZEK, 1901) from South America, as it has 11 or 12 antennular segments, a naked inner margin of the caudal rami, a relatively short dorsal caudal seta, and subequal apical spines of leg 4 endopod (see REID, 1985; EINSLE, 1996). *Acanthocyclops dodsoni* n. sp. differs from *A. michaelseni* by its spine formula, the length of the inner terminal caudal seta, and the proportions of caudal rami and the genital somite.

This is the sixth record of species of *Acanthocyclops* in Mexico, after *A. vernalis* from states in northern and Central Mexico (Coahuila, Michoacán, Nuevo León, Tamaulipas, San Luis Potosí, Guerrero), *A. robustus* (Distrito Federal, Mexico, Nuevo León, Puebla, San Luis Potosí, and Aguascalientes), *A. exilis* (Aguascalientes?), *A. smithae* REID and SUÁREZ-MORALES (Quintana Roo), and *A. rebecca* FIERS and GHENNE, 2000 (LINDBERG, 1955; SUÁREZ-MORALES and REID, 1998; GRIMALDO-ORTEGA *et al.* 1998; REID and SUÁREZ-MORALES, 1999; FIERS *et al.*, 2000; DODSON and SILVA-BRIANO, 1996). Because of the conspicuous difference represented by the easily discernible character as is the number of antennular segments, it is improbable that records of either *A. robustus* or *A. vernalis* in Central and Northern Mexico could be confused with the new species. The only other record of an 11-segmented species, that of *A. exilis* from Aguascalientes (DODSON and SILVA-BRIANO, 1996) could not be checked, but it is possible that it is assignable to this new species.

Most of the known species of *Acanthocyclops* occur mainly in temperate and subarctic latitudes in Eurasia and North and South America (see EINSLE, 1996; MIRABDULLAYEV and DEFAYE, 2002, 2004; Table 2). Records of *A. vernalis* s.l. and *A. robustus* s.l. have been reported from tropical and subtropical areas, including North Africa, Thailand, Ecuador, Bolivia, and Peru (DUSSART and DEFAYE, 1985; REID, 1985). Because of the morphological plasticity of this clade, it is possible that some of these records may refer to cryptic, undescribed taxa. The diversity of the Mexican fauna of *Acanthocyclops*, particularly in the neotropical region, could be underestimated. Recently, MIRABDULLAYEV and DEFAYE (2002, 2004), based on their redescription of *A. robustus*, described two new species from this species complex and established the occurrence of *A. robustus* in Canada and the United States, therefore, it is possible that records of this species from tropical and subtropical latitudes, could well be representing undescribed forms.

The only true tropical species of *Acanthocyclops* currently known are *A. smithae* from the Yucatan Peninsula, Honduras in Central America, possibly distributed also in Cuba, and *A. rebecca* from the Yucatan Peninsula. Both species are members of the taxonomically complex *vernalis-robustus* clade (REID and SUÁREZ-MORALES, 1999; FIERS *et al.*, 2000).

Apparently, the new species has mixed affinities; partly with a group of species with 11 or 12-segmented antennules, all known exclusively from the Nearctic region: the *venustus* group in North America (*A. montana*, *A. venustus*, *A. capillatus*). Besides the number of antennular segments, only the absence of an indentation on the first endopodal segment of the fourth leg links this species to the *venustus* group. On the other hand, another set of characters suggest that despite the number of segments, the new species could be more related to another Nearctic group, the *vernalis-robustus* clade, whose members bear 17-segmented

Table 2. Environment and geographical areas in which the American species of *Acanthocyclops* have been recorded. U.S. = United States of America; Mex. = Mexico; Can = Canada; N.A. = North America; S.A. = South America.

Species	Habitat	Subregion/Area	Reference
<i>A. capillatus</i>	ponds	Subarctic	EINSLE (1996)
<i>A. carolinianus</i>	ponds	Northwest U.S.	YEATMAN (1944)
<i>A. columbiensis</i>	acidic freshwater wetlands	Northwest U.S.	REID (1990b)
<i>A. dodsoni</i> n. sp.	dam	Central Mexico	this work
<i>A. exilis</i>	ponds	Northwest U.S.	COKER (1934)
<i>A. michaelseni</i>	ponds, lakes	Subantarctic, temperate S.A.	REID (1985)
<i>A. montana</i>	groundwater, wells	Northeast U.S.	REID <i>et al.</i> (1991)
<i>A. parasensitivus</i>	ponds	Northeast U.S.	REID (1998)
<i>A. parvulus</i>	groundwater	Northwest U.S.	STRAYER (1988)
<i>A. pennaki</i>	ponds, groundwater	Central U.S.	REID (1992)
<i>A. rebecca</i>	temporal pond	Southeast Mexico	FIERS <i>et al.</i> (2000)
<i>A. robustus</i>	ponds, lakes	N.A., Mex., S.A.	EINSLE (1996)
<i>A. smithae</i>	fishpond, muddy stream	South Mex, Honduras, Cuba?	REID and SUÁREZ-MORALES (1999)
<i>A. venustoides</i>	marsh habitats, meadows	Northwest U.S.	EINSLE (1996)
<i>A. vernalis</i>	ponds, groundwater, lakes	N.A., Mex., S.A.	EINSLE (1996)

antennules. These other characters include the setal (4444) and spine (3444) formulas, spinulated anal somite, inner caudal seta shorter than ramus, lateral setae of distal articles ornamented or transformed into spines. The number of antennular segments alone is not sufficient to support a relationship between taxa; i.e., according to EINSLE (1996), *A. muscicola* has 12 or 13-segmented antennules but it is closely related to *A. vernalis*. According to EINSLE (1996), the presence of modified setae on the swimming legs is relatively common in the *vernalis-robustus* clade. This important character, present in the new species, has been observed also in *A. smithae*, clearly a member of this clade (REID and SUÁREZ-MORALES, 1999), and in *A. muscicola* (see EINSLE, 1996).

The finding of this species, with a peculiar combination of characters, but with a clear affinity to Nearctic forms, is significant in regard to the biogeography of *Acanthocyclops* in the Americas. According to SUÁREZ-MORALES *et al.* (2004) the genus may have invaded parts of Mexico from the Nearctic region; they speculated that ancestral members of the *vernalis-robustus* clade could have colonized southern Mexico and upper Central America by dispersing from temperate areas of North America to reach South America. The wide distribution of *A. robustus*-like forms in Mexico, and the absence of both this species and the genus from lower Central America and northern South America, suggest that this ancestral form could have been present in southern Mexico as early as the Paleocene, when northern and central Mexico were connected and Central America was isolated. The ancestors of this clade might have had intermittent local dispersal events between marine transgressions, when the Yucatan and Central America land emerged, but because of the geological instability of the area, they did not disperse farther southwards into South America at that time. The wide distribution of the *vernalis-robustus* clade in southern United States (BRUNO *et al.*, 2005), and in central and northern Mexico is in contrast with the few isolated records of the genus from south and southeast Mexico (see SUÁREZ-MORALES *et al.*, 2004).

Ancestral populations of this clade could have been distributed in central and southern Mexico, both areas connected with North America and uncovered by the sea since the late Paleozoic. Members of the *vernalis-robustus* clade were clearly most successful in disper-

sal and speciation through local vicariant processes, as inferred from the fact that the only two true neotropical forms of the genus belong to this *vernalis-robustus* clade (REID and SUÁREZ-MORALES, 1999; FIERS *et al.*, 2000). It is likely that the *vernalis-robustus* clade spread into Northern and Central Mexico at different times; it is speculated that some species became extinct or were displaced, thus resulting in widely disjunct patterns. Therefore, *A. dodsoni* n. sp. could be the remain of radiation attempts by these Nearctic ancestors, possibly related to post-glacial repopulation, as all northern and central Mexico were affected by glaciations. A similar distributional pattern was described by GRANADOS-RAMÍREZ and SUÁREZ-MORALES (2003) to explain the occurrence of a Nearctic genus of Diaptomidae that was found isolated in central Mexico; they also suggested dispersal routes from North America to reach central Mexico, based on the theoretical patterns described by BĂNĂRESCU (1991). The presence of *A. dodsoni* n. sp. in a recent water body (the dam was built in the 1920's) suggests the possibility of dispersal from populations of the same general geographical area.

In the Americas, the genus *Acanthocyclops* has been recorded in a wide variety of environments, including hypogean habitats, acidic freshwater wetlands, meadows, and small temporary ponds (Table 2). Species of *Acanthocyclops* with 11–12 segmented antennules are frequently found in interstitial and groundwater environments (see EINSLE, 1996); contrastingly, the new species was found in a large dam, the type of environment in which species of the *vernalis-robustus* clade are commonly found.

Key for the identification of the species of *Acanthocyclops* recorded in Mexico (see also REID (1985), EINSLE (1996), REID and SUÁREZ-MORALES (1999), and FIERS *et al.* (2000) for additional characters):

- 1A. Females with less than 17 (commonly 11–12) antennular segments ... 2
- 1B. Females with 17-segmented antennules ... 3
- 2A. Terminal spines of third endopod of leg 4 unequal, outer spine twice as long as inner spine; inner terminal caudal seta longer than ramus; spine formula of third exopodal segment of legs 1–4 as 2333 ... *A. exilis*.
- 2B. Terminal spines of third endopod of leg 4 subequal; inner terminal caudal seta shorter than ramus; spine formula of third exopodal segment of legs 1–4 as 3444. ... *A. dodsoni* n.sp.
- 3A. Caudal rami elongated, more than 4 (up to 6, and even 10 in *A. vernalis* from Kamchatka and Japan: *Ishida*, 1998) times longer than wide; dorsal seta shorter than ramus; setae on third endopodal segment of legs 3 and 4 unmodified 4
- 3B. Caudal rami around 3 times longer than wide ... 5
- 4A. Inner terminal caudal seta about half the length of ramus; proximal part of genital somite forming angular chitinous process ... *A. vernalis* (records of this species in Mexico could represent cryptic species of this species complex).
- 4B. Inner terminal caudal seta more than half the length of ramus; proximal part of genital somite rounded ... *A. robustus* species complex (some of the tropical and subtropical records of this species could refer to undescribed forms of this species complex: see MIRABDULLAYEV and DEFAYE (2002, 2004)).
- 5A. Antennal basis with rows of short, slender spines on frontal and caudal surfaces; middle terminal caudal seta stout; dorsal seta as long as ramus; modified setae on third endopodal segment of legs 3 and 4; spine formula 3444 ... *A. smithae*.
- 5B. Antennal basis with rows of coarse spines on frontal and caudal surfaces; middle terminal caudal seta normal; dorsal seta slightly shorter than ramus; unmodified setae on third endopodal segment of legs 3 and 4; spine formula 2333 ... *A. rebecae*.

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6. References

- BĂNĂRESCU, P., 1991: Zoogeography of Freshwaters. 2. Distribution and Dispersal of Freshwater Animals in North America and Eurasia. Aula-Verlag. Wiesbaden, 1256–1282.
- BOXSHALL, G. A. and S. H. HALSEY, 2004: An Introduction to Copepod Diversity. The Ray Society 166. London 966 pp.
- BRUNO, M. C., REID, J. W. and S. A. PERRY, 2005: A list and identification key for the freshwater, free-living copepods of Florida (USA). – *J. Crust. Biol.* **25**: 384–400.
- COKER, R. E., 1934: Nearly related copepods differentiated physiologically as well as morphologically (*Cyclops vernalis* FISCHER, *C. venustoides*, n. sp. and *C. exilis* n. sp.). – *J. Elisha Mitchell Sci. Soc.* **49**: 264–284.
- DODSON, S. I., 1994: Morphological analysis of Wisconsin (USA) species of the *Acanthocyclops vernalis* group (Copepoda: Cyclopoida). – *J. Crust. Biol.* **14**: 113–131.
- DODSON, S. I. and M. SILVA-BRIANO, 1996: Crustacean zooplankton species richness and associations in reservoirs and ponds of Aguascalientes state, Mexico. – *Hydrobiologia* **325**: 163–172.
- DODSON, S. I., A. K. GRISHANIN, K. GROSS and G. A. WYNGAARD, 2003: Morphological analysis of some cryptic species in the *Acanthocyclops vernalis* species complex from North America. – *Hydrobiologia* **500**: 131–143.
- DUSSART, B. H. and D. DEFAYE, 1985: Répertoire mondial des copépodes cyclopoïdes. C.N.R.S. Paris. 236 pp.
- DUSSART, B. H. and D. DEFAYE, 2001: Introduction to the Copepoda. (2nd edition) (revised and enlarged). – *In*: H. J. F. DUMONT (ed.), Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. SPB Academic Publishing, The Hague. 289 pp.
- EINSLER, U., 1996: Copepoda: Cyclopoida. Genera *Cyclops*, *Megacyclops*, *Acanthocyclops*. – *In*: H. J. F. DUMONT (ed.), Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. SPB Academic Publishing, The Netherlands, The Hague. **10**: 1–82.
- FIERS, F., V. GHENNE and E. SUÁREZ-MORALES, 2000: New species of continental copepods (Crustacea, Cyclopoida) from the Yucatan Peninsula, Mexico. – *Stud. Neotrop. Faun. Environ.* **35**: 209–251.
- GRANADOS-RAMÍREZ, J. G. and E. SUÁREZ-MORALES, 2003: A new *Hesperodiptomus* LIGHT (Copepoda, Calanoida, Diaptomidae) from Mexico with comments on the distribution of the genus. – *J. Plankton Res.* **25**: 1383–1395.
- GRIMALDO-ORTEGA, D., M. ELÍAS-GUTIÉRREZ, M. CAMACHO-LEMUS and J. CIROS-PÉREZ, 1998: Additions to Mexican freshwater copepods with the description of the female *Leptodiptomus mexicanus* (MARSH). – *J. Mar. Syst.* **15**: 381–390.
- GRISHANIN, A. K., E. M. RASCH, S. I. DODSON and G. A. WYNGAARD, 2005: Variability in genetic architecture of the cryptic species complex of *Acanthocyclops vernalis* (Copepoda). I. Evidence from karyotypes, genome size, and ribosomal DNA sequences. – *J. Crust. Biol.* **25**: 375–383.
- HUYS, R. and G. A. BOXSHALL, 1990: Copepod Evolution. The Ray Society, London. 468 pp.
- ISHIDA, T., 1998: Freshwater copepods from the east coast of Kamchatka Peninsula, Russia. – *J. Mar. Syst.* **15**: 391–396.
- LINDBERG, K., 1955: Cyclopoïdes (Crustacés copépodes) du Mexique. – *Arch. Zool.* **7**: 459–489.
- MIRABDULLAYEV, I. M. and D. DEFAYE, 2002: On the taxonomy of the *Acanthocyclops robustus* species complex (Copepoda, Cyclopidae) 1. *Acanthocyclops robustus* (G. O. SARS, 1863) and *Acanthocyclops trajani* n. sp. – *Selevinia* **1–4**: 7–20.
- MIRABDULLAYEV, I. M. and D. DEFAYE, 2004: On the taxonomy of the *Acanthocyclops robustus* species complex (Copepoda, Cyclopidae). *Acanthocyclops brevispinosus* and *A. einslei* sp. n. – *Vestnik Zool.* **38**: 27–37.

- REID, J. W., 1985: Chave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da Ordem Cyclopoida (Crustacea, Copepoda). – Bolm. Zool. Univ. São Paulo **9**: 17–143.
- REID, J. W., 1990a: Continental and coastal free-living Copepoda (Crustacea) of Mexico, Central America and the Caribbean region. – In: D. NAVARRO and J. G. ROBINSON (eds.), *Diversidad Biológica en la Reserva de la Biosfera de Sian Ka'an*, Quintana Roo, México. CIQRO/Univ. of Florida: 175–213.
- REID, J. W., 1990b: Copepoda (Crustacea) from acidic wetlands in the District of Columbia and Maryland, including a description of *Acanthocyclops columbiensis*, new species. – Trans. Am. Microscop. Soc. **109**: 174–180.
- REID, J. W., E. B. REED, J. V. WARD, N. J. VOELZ and J. A. STANFORD, 1991: *Diacyclops languidoides* (LILLJEBORG, 1901) s.l. and *Acanthocyclops montana*, new species (Copepoda, Cyclopoida), from groundwater in Montana, USA. – Hydrobiologia, **218**: 133–149.
- REID, J. W., 1992: *Acanthocyclops pennaki* n. sp. (Copepoda: Cyclopoida) from the hyporheic zone of the South Platte River, Colorado, USA. – Trans. Am. Microscop. Soc. **111**: 267–277.
- REID, J. W., 1998: How “cosmopolitan” are the continental cyclopoid copepods? Comparison of North American and Eurasian faunas, with description of *Acanthocyclops parasensitivus* sp.n. (Copepoda: Cyclopoida) from the USA. – Zool. Anz. **236**: 109–118.
- REID, J. W. and E. SUÁREZ-MORALES, 1999: A new, neotropical species of *Acanthocyclops* (Copepoda: Cyclopoida: Cyclopidae). – Beaufortia, Zoological Museum, Amsterdam **49**: 37–45.
- REID, J. W., 2003: A technique for observing copepods. – In: H. UEDA and J. W. REID (eds.), *Copepoda Cyclopoida Genera Mesocyclops and Thermocyclops*. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. 20. Backhuys Publ. Amsterdam: 8.
- ROCHA, C. E., 1998: New morphological characters useful to the taxonomy of the genus *Microcyclops* (Copepoda, Cyclopoida). – J. Mar. Syst. **15**: 425–431.
- ROCHA, C. E. and M. J. BOTELHO, 1998: Maxillopoda-Copepoda. Cyclopoida. – In: P. S. YOUNG (ed.), *Catalogue of Crustacea of Brazil*. Museu Nacional, Rio de Janeiro: 129–166.
- SCHUTZE, M. L., C. E. F. ROCHA and G. A. BOXSHALL, 2000: Antennular development during the copepodid phase in the family Cyclopidae (Copepoda, Cyclopoida). – Zoosystema **22**: 749–806.
- SUÁREZ-MORALES, E. and J. W. REID, 1998: An updated list of the free-living freshwater copepods (Crustacea) of Mexico. – Southwest. Nat. **43**: 256–265.
- SUÁREZ-MORALES, E., J. W. REID, F. FIERS and T. M. ILIFFE, 2004: Historical biogeography and distribution of the freshwater cyclopine copepods (Copepoda, Cyclopoida, Cyclopinae) of the Yucatan Peninsula, Mexico. – J. Biogeogr. **31**: 1051–1063.
- STRAYER, D., 1988: New and rare copepods (Cyclopoida and Harpacticoida) from freshwater interstitial habitats in Southeastern New York. – Stygologia **4**: 41–55.
- WILLIAMSON, C. E. and J. W. REID, 2001: Copepoda. – In: J. H. THORPE and A. P. COVICH (eds.), *Ecology and Classification of North American Freshwater Invertebrates*. 2nd edition. Academic Press, San Diego: 915–954.
- YEATMAN, H. C., 1944: American cyclopoid copepods of the *viridis-vernalis* group (including a description of *Cyclops carolinianus* n. sp.). – Am. Midl. Nat. **32**: 1–90.
- YEATMAN, H. C., 1959: Free-living Copepoda: Cyclopoida. – In: W. T. EDMONSON (ed.), *Ward and Whipple's Freshwater Biology*, 2nd. Ed. Wiley, New York: 795–815.

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